Auxin and ethylene regulation of fruit set

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A B S T R A C T

With the forecasted fast increase in world population and global climate change, providing sufficient amounts of quality food becomes a major challenge for human society. Seed and fruit crop yield is determined by developmental processes including flower initiation, pollen fertility and fruit set. Fruit set is defined as the transition from flower to young fruit, a key step in the development of sexually reproducing higher plants. Plant hormones have important roles during flower pollination and fertilization, leading to fruit set. Moreover, it is well established that fruit set can be triggered by phytohormones like auxin and gibberellins (GAs), in the absence of fertilization, both hormones being commonly used to produce parthenocarpic fruits and to increase fruit yield. Additionally, a number of studies highlighted the role of ethylene in plant reproductive organ development. The present review integrates current knowledge on the roles of auxin and ethylene in different steps of the fruit set process with a specific emphasis on the interactions between the two hormones. A deeper understanding of the interplay between auxin and ethylene may provide new leads towards designing strategies for a better control of fruit initiation and ultimately yield.

1. Introduction

Fruit set is known as the initial step of fruit development in sexual reproduction of flowering plants, a process by which the flower turns into a fruit. The transition from flower to fruit corresponds to a developmental shift that is naturally triggered upon flower fertilization and leading to the activation of a high number of metabolic pathways and anatomical transformations that result in the change in organ identity. Fruit set relies on successful pollination of the stigma, followed by pollen germination and subsequent growth of the pollen tube towards the ovule [1]. Then, the fertilization of the ovule triggers the division and expansion of the cells surrounding the embryo [1], and it is widely accepted that the whole process is regulated by plant growth substances, such as phytohormones, with auxin playing a pivotal role in the regulation of this developmental shift [2,3].

Notably, the role of auxins in the development of fruit from unfertilized ovules, a process called parthenocarpy, has been largely documented, and it was proposed that auxin can serve as alternative signal replacing pollination and fertilization to initiate the fruit growth program. It was also shown that auxins interact with the GAs, and that both hormones stimulate cell division and expansion during the fruit set. In particular, auxin was reported to increase GA content, by upregulating GA biosynthesis genes [4]. Further insights into the molecular mechanisms involving the two hormones in the regulation of fruit initiation were provided by the discovery of SlARF7, an auxin response factor, which mediates a crosstalk between auxin and GA signaling [5]. Recent studies showed that abscisic acid also plays an important role in regulating tomato fruit set, further adding to the complexity of the network that regulates this process [1,4,5].

Ethylene has been recognized as an important hormone in several plant development processes and ethylene production increases in the flowers of many plant species after pollination [6], although it was also reported that ethylene biosynthesis starts to decrease once fruit set is completed [3]. However, our understanding of the function of ethylene during carpel development and fruit set in tomato is mostly limited to transcriptome profiling of tomato ovaries which revealed alterations in a high number of ethylene related genes involved in the flower-to-fruit transition [1,7]. The role of ethylene in pollination-independent fruit set has also been suggested based on treatments with the ethylene perception inhibitors, silver thiosulphate and 1-methylcyclopropene (1-MCP) or with the ethylene biosynthesis inhibitor, 2-aminoethoxyvinyl glycine, that leads to parthenocarpic fruit formation [8]. Taken together, these findings support the idea that ethylene plays an active role in the regulation of fruit set, although its precise contribution to this process and its mode of action remain to be further clarified.

The present review addresses various aspects of the regulation of the

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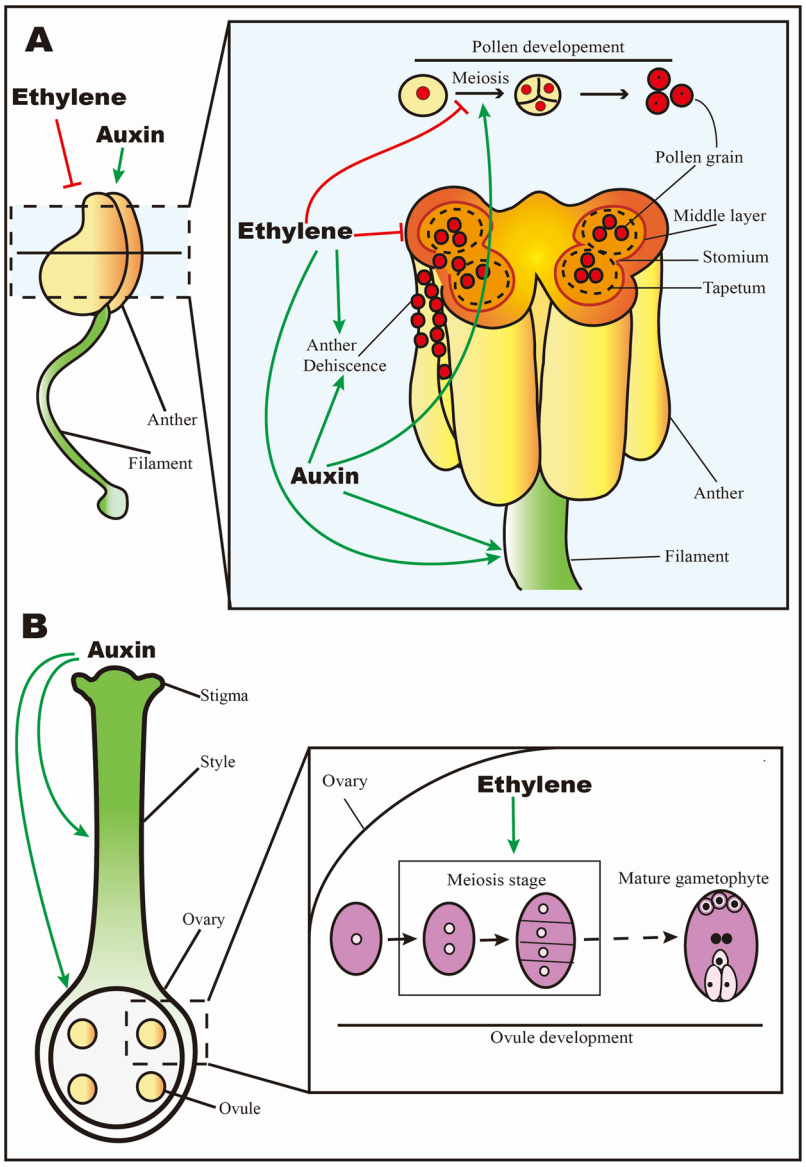

Fig. 1. Ethylene and auxin regulate the development of plant male and female organs.

Green lines stand for positive regulations. Red lines stand for negative regulations. ***(A) Ethylene and auxin regulate stamen formation and development.*** This panel illustrates ethylene and auxin roles detailed in the 2.1 paragraph. Briefly, ethylene and auxin participate in pollen formation and development, and play important roles at the meiosis stage; ethylene induces the programmed cell death (PCD) of the tapetum and middle layer, which leads to anther dehiscence and pollen release; auxin may induce anther dehiscence; ethylene and auxin may promote filament elongation. ***(B) Ethylene and auxin regulates pistil formation and development.*** This panel illustrates ethylene and auxin roles detailed in the 2.2 paragraph. Briefly, ethylene induces the early stage of ovule development; auxin synthesis in apical domain of gynoecium plays an important role in style and ovary formation.

fruit set by ethylene and auxin, and provides new leads towards unravelling the mechanisms underlying this hormonal crosstalk. For a better clarity, the roles of ethylene and auxin are considered at different stages of fruit set, including sexual organ formation, pollination, fertilization, and in parthenocarpic fruit formation.

1.1. Auxin biosynthesis, transport and signaling pathway

In higher plants, there are two major routes for indole acetic acid (IAA) biosynthesis: the tryptophan (Trp)-dependent and the Trp-independent pathways [9–11]. In the Trp-dependent pathways, IAA is biosynthesized from L-Trp by a two-step process: the first step corresponds to the transformation of Trp to indole-3-pyruvic acid (IPA) catalyzed by TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS (TAA/TAR) family, then IPA is decarboxylated by YUCCA flavin monooxygenase enzymes to form IAA [10]. The Trp-independent pathway was discovered two decades ago. It assumes that IAA can be produced *de novo* without Trp [9]. In this pathway, the indole-3-glycerol phosphate (IGP) is converted to indole by indole synthase, which initiates IAA synthesis without Trp [11].

Auxin transport can be operated either by diffusion (passive movement) or by specific transporters (active movement) [12]. IAA is protonated in the apoplasmic compartment, crossing the plasma membrane to diffuse into the cell. Once in the cytosol, IAA is mainly deprotonated due to the higher pH, and the resulting charged molecule (IAA-) is membrane impermeable. Then transporters are required to help auxins to to cross the plasma membranes. Several auxin carrier families have been identified, such as AUXIN-RESISTANT 1/LIKE AUX1 (AUX1/LAX) influx carriers, PIN-FORMED (PIN) and ATP-BINDING CASSETTE (ABCB) auxin efflux carriers which mediate auxin distribution in and between cells [12].

Auxin is perceived by the cytoplasmic F-box-domain-containing proteins named TRANSPORT INHIBITOR RESPONSE1/AUXIN SIGNALING F-BOX (TIR1/AFB) [13]. The pathway linking auxin perception to gene expression involves the ubiquitination of AUXIN RESISTANT/INDOLE-3-ACETIC ACID INDUCIBLE (Aux/IAA) proteins by the TIR1/AFB subunit of the SCFTIR1/AFB ubiquitin ligase and their degradation by the 26S proteasome. Then the Aux/IAA-mediated inhibition of AUXIN RESPONSE FACTORs (ARFs) is released, which allows ARFs to modulate the expression of their downstream target genes, known as auxin-responsive genes [14].

1.2. Ethylene biosynthesis and signaling pathways

The biosynthesis of ethylene includes three steps, the first leading from methionine to S-Adenosyl-Methionine (SAM) catalyzed by the S-adenosyl-methionine synthetase (SAM synthetase), the second transforming SAM into 1-aminocyclopropane-1-carboxylic acid (ACC) by ACC synthase (ACS) and finally the production of ethylene from ACC by ACC oxidase (ACO). The pool of ACC is also regulated by conjugation via ACC acyl-transferases leading to the formation of ACC derivatives like malonyl-ACC, glutamyl-ACC, and jasmonyl-ACC, which affects the pools of free ACC and hence ethylene biosynthesis [15].

Ethylene is perceived by different ethylene receptor proteins (ETRs), located in the endoplasmic reticulum membrane. The number of ETRs varies among species with five receptors reported in Arabidopsis, ETR1, ETR2, EIN4, ERS1, and ERS2 [16] and seven ethylene receptors in the tomato, ETR1, ETR2, ETR3, ETR4, ETR5, ETR6, and ETR7, each having a distinct pattern of expression throughout development and in response to external stimuli [17]. The ETRs are negative regulators of ethylene responses and interact with other protein partners like CONSTITUTIVE TRIPLE RESPONSE (CTRs) protein kinases which are also negative regulators of the downstream signal. In the absence of ethylene, the ETR-CTR complex maintains the ETHYLENE INSENSITIVE2 protein (EIN2) in a phosphorylated state at its C-terminus domain which prevents its cleavage [18]. In the presence of ethylene, the protein complex (ETR-CTRs) is dephosphorylated and inactivated, thus causing the cleavage of the EIN2 C-terminus domain by proteases, and this C-terminus domain moves into the nucleus, promoting the accumulation of EIN3/EILs by preventing its degradation via EBF1 and EBF2 [16]. The EIN3/EIL3 proteins activate the transcription of ethylene response factors (ERFs), which in turn lead to expression of hundreds of ethylene responsive genes, through binding to GCC-boxes and other cis-acting elements [17,18].

Ethylene and auxin can interact synergistically or antagonistically to control a variety of plant development processes, such as fruit development, fruit ripening, root formation and hypocotyl elongation [19,20].

2. Ethylene and auxin regulate the formation of plant male and female organs

2.1. Male reproductive organs

In flowering plants, the stamen male reproductive organ is made of the filament and the anther where pollen is produced (Fig. 1A). The formation and development of normal stamens are essential for male fertility, and therefore for successful fruit set. A number of studies highlighted the expression dynamics of genes encoding various components of ethylene signaling and responses in male reproductive organs suggesting an active role for ethylene in pollen development [21,22]. For instance, in Arabidopsis, *AtEIN4* and *AtERS2* exhibit high expression at the transcript level in stamen, including pollen and tapetum cells. These latter form a specialized cell layer feeding the developing pollen grains. High expression of ethylene receptors in these tissues suggests that ethylene is important in these processes [21]. *AtERS2* gene shows a similar expression pattern to the ethylene receptor gene *Os-ERS1* in rice that is up-regulated during early pollen development, corresponding to meiotic and microspore stages [22]. In tomato, the ethylene production capacity of pollen grains is consistent with the expression of ethylene biosynthesis and signaling genes in these tissues [23]. Moreover, the application of high concentration of exogenous ethylene on male gametophyte induces the degradation of the generative cell at meiosis stage resulting in male sterility [24]. Regarding auxins, many studies showed that they are involved in pollen development. For example, IAA accumulates in anthers prior to pollination, specifically in pollen grains, tapetum, endothecium and epidermis cells of anthers [25]. Moreover, the repression of the *iaaL* gene encoding indoleacetic acid–lysine synthetase, which converts free IAA to its inactive form IAA-lysine, results in low free IAA content in anther and reduced pollen viability due to defective mitosis [25]. In tomato, the down-regulation of *SlPIN8*, a gene encoding an auxin-transporter specifically expressed in tomato pollen, resulted in up to 80 % abnormal pollen grains with extremely poor viability [26]. Altogether, these data suggest that ethylene and auxin play important roles in pollen development, and that high amount of ethylene may have detrimental effect on the process.

Additionally, several studies showed that ethylene has critical roles in pollen release. The process of anther dehiscence involves two main steps sequentially consisting of (i) degeneration of the middle layer and tapetum; (ii) breakage of the anther wall at the region of stomium between the two locules of each anther [27]. It has been reported, using transgenetic tabacco plants, that the mutant melon ethylene receptor gene *Cm-ERS1/H70A* exhibits delay in tapetum programmed cell death, resulting in the production of abnormal pollen [28]. In the Arabidopsis ethylene insensitive mutant *etr1-1*, the (i) stomium cells showed delayed degeneration and then (ii) anther dehiscence is delayed [29]. These two events have been related to ethylene production peaks in petunia [24]. Moreover, application of ethylene-perception inhibitors 2,5-norbornadiene and 1-MCP impaired anther dehiscence in petunia and tobacco, respectively, whereas ethylene treatment accelerated this process [29]. Similarly, in Petunia, the down-regulation lines of ethylene receptor gene *PhETR2* hastened stomium degeneration and anther dehiscence, making these process happened before anthesis, which is earlier than in wild type, indicating that PhETR2 regulates the timing of anther dehiscence [30]. This seems to indicate that through promoting anther dehiscence, ethylene promotes pollen release. It was shown that auxin also involves in anther dehiscence process, the quadruple mutant *tir1/ afb1/ afb2/ afb3* displaying auxin perception defects shows early anther dehiscence due to premature lignification of endothecium cell walls and precocious breakage of the stomium [31].

Regarding male sterility, ethylene and auxin also appear to be involved in the arrest of stamen development [29–36]. In Arabidopsis, it shows the stamen development arrest in *CsACO2* overexpressed lines, suggesting that the increase in ethylene production inhibits stamen development [32]. Also, down regulation of cucumber *ETR1* ethylene receptor gene induced abnormal stamen development leading to female flower only [33]. Moreover, it was shown in tobacco that ethylene perception is critical for filament elongation [34]. However, it was shown that auxin positively regulates stamen development, including filament elongation and pollen maturation [34–36]. Indeed, in the Arabidopsis *yuc2-yuc6* double mutant, the down regulation of auxin biosynthesis caused the failure of filament elongation and pollen maturation [35], similar observations were performed when auxin perception were altered [34]. When auxin transport is affected, in Arabidopsis *pin1-1* and *pin1-2* mutants, no stamen developed [36].

Finally, cross-talks between auxin and ethylene have been observed in *Gaillardia grandiflora* at the stamen level, as auxin promotes pollen tube elongation and ethylene production at the same stage. This auxin-induced ethylene has an important role in the later stigma opening stage [37]. Taken together, these findings support the idea that ethylene and auxin play important roles in male reproductive organs of higher plants.

2.2. Female reproductive organs

In female reproductive organ, the pistil (Fig. 1B) provides protection for the ovules, enables pollen capture and pollen tube guidance, and supports self- and inter-specific incompatibility. Following fertilization of the ovules, in true fruit, such as grape and tomato, the gynoecium develops into a fruit, which protects the developing seeds and ultimately facilitates mature seed dispersal; in false fruit, such as apple and pears, the fruit derives from other flower parts, after fertilization [38]. Gynoecium development involves the differentiation of specialized

functional modules, including the stigma which forms at the apex of pistil, and will capture and stimulate the pollen grain germination [39]. The style or pistil is located immediately below the stigma and contains transmitting tissues that conduct pollen tubes to the ovary, the basal structure containing the ovules [39]. The formation of normal and functional gynoecium is essential for female fertility, and hence for successful fruit set. The role of ethylene in female gametophyte development, and ultimately in promoting ovule fertilization, has been addressed in several studies [39,40]. In tobacco, the ethylene biosynthesis gene, *ACO1* is expressed during early stages of ovule development (meiosis stage), and its silencing results in the arrest of ovule development and failure to reach the maturity stage. Similar effect was obtained by the application of the ethylene biosynthesis inhibitor, silver thiosulfate [40]. Notably, upon exogenous ethylene treatment, the ovules recover their functionality and restore the guidance of pollen tubes to the ovule micropyle [40].

The role of auxin in female reproductive organ was revealed through the characterization of the *AGAMOUS*-clade of MADS-box genes showing that members of MADS-box B 3 domain transcription factors *NGATHA* (*NGA1* to *NGA4*) play an essential role in style development; the loss-of-function of these four *NGA* genes results in complete loss of style and stigma development, and this phenotype is due to the failure of activating *YUCCA*mediated auxin synthesis in apical domain of gynoecium [41]. These studies emphasize the role of auxin in apical-basal gynoecium pattern.

3. Ethylene and auxin regulate pollination-dependent fruit set

3.1. Pollen germination and tube growth

In plants, pollination refers to the release of the pollen from the anther and its deposition at the surface of the stigma (Fig. 2A). When the pollen grain rehydrates and germinates on the stigma, the pollen tube starts to grow inside the style. The pollen grain contains a nucleus and a generative cell, which divides into two sperm cells [42]. The pollen tube grows navigating through transmitting tissue in the style towards the ovule where it releases the sperm cells for double fertilization [43]. The reality and the nature of the pollination signal remains a matter of debate, even though auxin, or ACC, have been proposed as the acting molecular signals [44,45]. In petunia, the level of ACC increases 100 fold in mature pollen grain and in anthers one day before anthesis [46]. In tomato, it was shown that pollen grain has the capacity to produce and sense ethylene before germination, as suggested by the expression of several ethylene biosynthesis and signaling genes including *SlACS3*, *SlACS11*, *SlETR3* and *SlCTR2* [23]. Nevertheless, exogenous application of ACC in flowers cannot induce the post-pollination development [47]. When applying the synthetic auxin, NAA, to the stigma of orchids, the ethylene production was stimulated in flowers [45]. Although these findings support the idea that auxin and ethylene are important for pollination initiation, other factors might also contribute to the regulation of this process.

It was suggested that auxins regulate pollen germination [48,49]. In support to this hypothesis, IAA accumulates at high levels in the stigma when most pollen grains germinate [50] and, free IAA is high in the growing tip of the pollen tube where it was suggested to promote rapid pollen tube growth [49]. It has also been reported that IAA treatment results in straighter and more slender pollen tube growth which facilitates its elongation [51,52]. Notably, plasma membrane H^+ ATPase has been shown to interact with 14-3-3 proteins, an interaction that is important for pollen germination [53]. However, when the pollen tube enters the style, the amount of auxin decreases in the style tissues [50].

The growth and elongation of the pollen tube is essential for successful fertilization and subsequent fruit set since it carries two male gametes to the ovary and ovule over a long distance in the pistil (Fig. 2B). The transmission tissues in the style play an important role in providing nutrition and mechanical support for pollen tube growth and, after pollination, transmission tissues begin to be malformed and deteriorate, which could provide nutrition to surrounding tissues [51]. In addition, the cellular degeneration of transmission tissues in the style provides more space, allowing the penetration of the pollen tube in the stigma. This degeneration facilitates the passage of pollen tube in the style to reach the ovary, and these events are considered as a programmed cell death process [51]. Several studies have shown the important role of ethylene in pollen tube growth [6,54]. Both ACC and ethylene have a role in the degeneration of transmitting tissues, by promoting the shortening of the polyA tail of some RNAs specific to these transmitting tissues [51]. On one hand, the treatment with 1-MCP reduces pollen tube growth in petunia [6]. On the other hand, it was shown that ethylene promotes pollen tube growth by increasing the relative amount of F-actin, which is important for the polarized growth of this tube [55]. Upon pollination, the increase in ethylene production reaches a maximum in the stigma and is associated with enhanced expression of *ACS* and *ACO* genes in the ovary. By contrast, control emasculated flowers did not exhibit such a change in ethylene production [56]. In orchid gynoecium, *ACS* and *ACO* genes reach an expression peak 24–48 h after pollination, and then decline [47], and similar expression patterns for *ACS* or *ACO* were observed in petunia and carnation [57].

3.2. Changes to ovary development

The presence of auxin and ethylene is required to initiate changes in ovary development and to induce ovule differentiation (Fig. 2C). It has been found that following pollination with fresh pollen, enhanced ethylene synthesis and auxin transport are necessary to initiate the egg cell differentiation in maize ovules [58]. Before fertilization, auxin production is suppressed by FIS-PRC2 in the central cell, and this suppression is released upon fertilization. In *fis* mutants impaired in the FIS-PRC2 block system, auxin biosynthesis is induced before fertilization and initiates autonomous endosperm formation [59].

In flowering plants, when the pollen tube reaches the ovule, two male sperm cells are released to fuse with two female gametes, the egg cell and the central cell (Fig. 2D). The fused egg cell will develop into an embryo, and the fused central cell will give the endosperm, which provides nutrition and support to embryo [60]. The two synergids are responsible for pollen tube attraction, but only one pollen tube will fertilize the ovule [61]. Recent studies demonstrate that ethylene signal is critical to prevent the attraction of a second pollen tube and it was shown that egg cell fertilization induces the activation of EIN3- and EIN2-dependent ethylene response pathway necessary for the programmed cell death of the synergid cell [62]. In addition, the over-accumulation of EIN3 in synergid cells leads to the block of pollen tube attraction [63]. Auxin has been suggested to regulate maize endosperm proliferation. A study in the maize mutant *defective endosperm18 (de18)* showed that IAA biosynthesis is impaired and the total cell number is lower in the endosperm, and the level of endoreduplication of the endosperm is reduced [64].

4. Ethylene and auxin roles in parthenocarpy

Parthenocarpy corresponds to the ovary development in the absence of pollination and fertilization [65]. In this regard, it is considered as a desirable agronomic trait to improve fruit set in adverse climate conditions. In addition, the seedless fruits due to parthenocarpic development are preferred by consumers [65]. It has long been known that applying synthetic phytohormones like auxin and gibberellic acid (GA) to unpollinated flower buds induces parthenocarpic fruit set [66]. However, exogenous application of plant hormones to get seedless fruits is costly, thus genetic engineering strategies are promoted, aiming at altering hormone biosynthesis or signaling in order to obtain parthenocarpic fruits. Pioneering work, in this domain, targeted the up-regulation of the *iaaM* gene to promote the synthesis of indolacetamide,

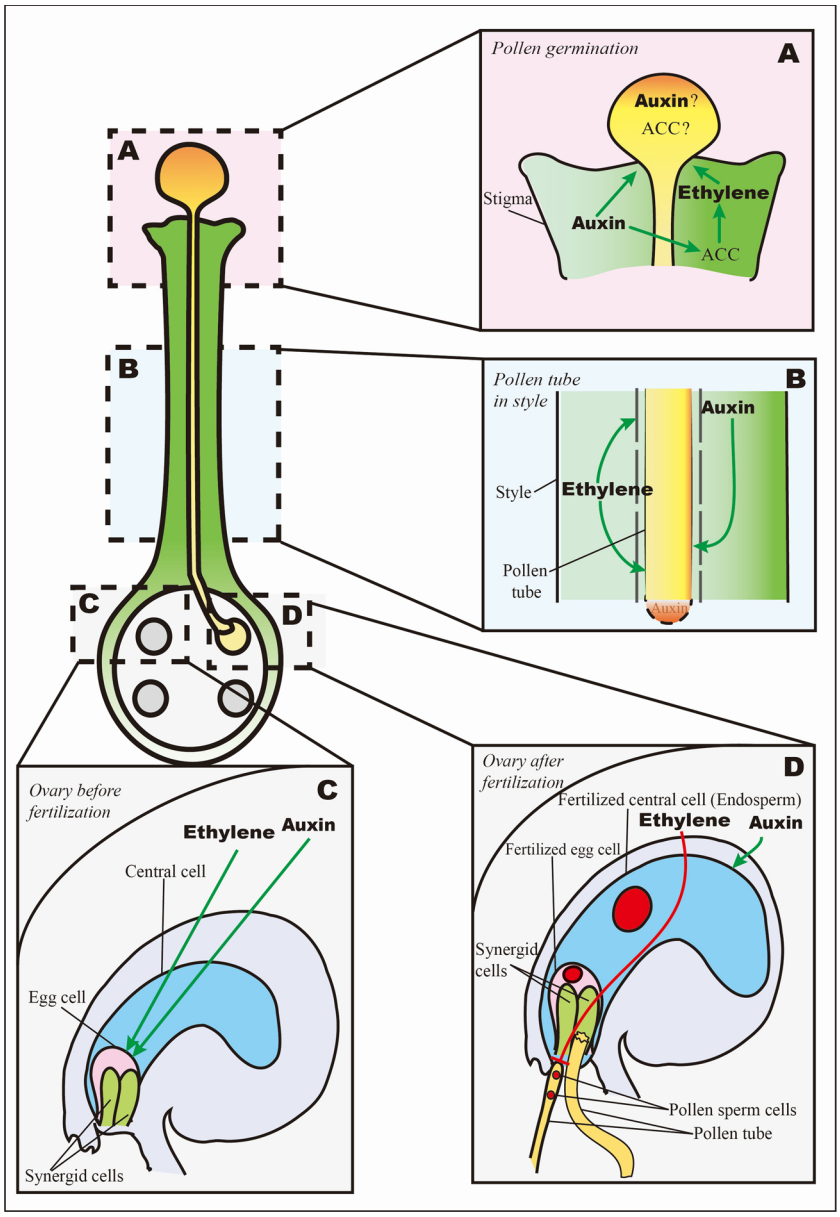

Fig. 2. Ethylene and auxin regulate plant pollination and fertilization processes.

Green lines stand for positive regulations. Red lines stand for negative regulations. ***(A) Pollen germination.*** This panel illustrates ethylene and auxin roles detailed in the 3.1 paragraph. Briefly, mature pollen grain contains ACC and auxin, which may induce pollen germination.
ethylene and auxin both induce pollen germination in stigma, and auxin stimulates ACC synthesis. ***(B) Pollen tube growth in style.*** This panel illustrates ethylene and auxin roles detailed in the 3.2 paragraph. Briefly, ethylene helps degradation of transmission tissues in the style, which facilitates pollen tube growth. Auxin accumulates in the tip of pollen tube, and this facilitates pollen tube growth. ***(C) Ovary before fertilization.*** This panel illustrates ethylene and auxin roles detailed in the 3.3 paragraph. Briefly, the increase of ethylene and auxin concentrations are necessary to initiate egg cells differentiation in ovules after pollination. ***(D) Ovary after fertilization.*** This panel illustrates ethylene and auxin roles detailed in the 3.4 paragraph. Briefly, ethylene promotes programmed cell death of synergid cell, which prevents second pollen tube attraction; auxin is important for endosperm development, especially in endoreduplication.

which can be converted to IAA [67]. The expression of this auxin biosynthesis gene, driven by the promoter of *DefH9*, a MADS-box gene expressed specifically in ovules, resulted in parthenocarpic fruit development in both tobacco and eggplant [67]. Thereafter, the same gene was used to obtain parthenocarpic fruit in several horticultural crops, like tomato and cucumber [68]. Another successful approach to produce parthenocarpic fruit dealt with the down-regulation of *SlIAA9,* encoding a negative regulator of auxin-dependent gene transcription [2]. Subsequently, the parthenocarpic trait was also achieved through up or down-regulation of members of auxin response factors in different species [69]. In Arabidopsis, the loss of function mutation of *AtARF8* produced dehiscent and parthenocarpic siliques [69]. In tomato, the down-regulation of *SlARF8* and *SlARF7* formed parthenocarpic fruit, and the over-expression of *SmARF8* in eggplant produced the same seedless trait [5,70,71]. Overall, auxin biosynthesis and signaling genes provide efficient targets to engineer parthenocarpic plants in a variety of species.

Most studies showed that ethylene acts as a negative regulator of parthenocarpy in plants [8]. For example, in Arabidopsis, ethylene is responsible for ovule senescence by preventing GA perception; hence, ethylene indirectly leads to the degradation of ovule tissues, thus reducing parthenocarpic fruit set [8]. On the other hand, preventing ethylene perception in emasculated flowers of tomato, either by using 1–MCP, or by using ethylene insensitive mutants (*etr1-1*), led to more parthenocarpic fruits [72]. Similarly, blocking ethylene synthesis, by using 2-aminoethoxyvinyl glycine, or blocking ethylene perception, by using silver thiosulphate, induced parthenocarpy in zucchini squash [73].

To date, there is no study focusing on the crosstalk of auxin and ethylene during parthenocarpic fruit set.

5. Conclusions and perspectives

A large set of data supports the notion that both ethylene and auxin play active roles in controlling the fruit set process, at different steps of the flower-to-fruit transition. But there is a need for research to detail the potential crosstalk between auxin and ethylene signals in the control of this transition. The two hormones impact all stages of stamen development, including elongation of stamen filament bringing anthers close to stigma, pollen maturation, and anther dehiscence to release

pollen on stigma. Proper completion of these events is critical to the formation and development of reproductive sexual organs and then to successful initiation of the fruit set process [74]. Ethylene and auxin are also involved in most events associated with the germination of pollen in the stigma, the growth of pollen tube through the transmission tissues in the style and finally the fertilization of the ovule. The use of mutant lines impaired in both auxin and ethylene responses will allow to better decipher the roles of auxin and ethylene in initiating and controlling the flower-to-fruit transition. By building on studies about crosstalk in other developmental processes, like root formation and hypocotyl elongation [20], future research will allow to further detail the dialogue engaged between the two hormones in the different phases of the fruit set. For example, it was shown that mutants altered in AUX1 and EIR1/AGR/PIN2 with impaired auxin transport, and those affected in TIR1 auxin receptor, exhibit ethylene insensitive root growth, which supports the idea of interdependence of both hormones [75,76]. More recently, it was reported that ERF109 binds directly to the promoters of *ASA1* and *YUC2* auxin biosynthesis genes, and ERF1 could bind with the promoter of *ASA1*, leading to auxin increase and ethylene-induced root growth inhibition [77,78]. Similarly, the expression of *Sl-IAA27* is regulated by direct binding of ERF.B3 to its promoter [79]. The regulation of *ACS* expression by ARFs, and of *TAA1* by EIN3 have been documented [80]. Finally, the impaired expression on *SlSAUR69* in the tomato results in altered auxin distribution and change in ethylene sensitivity [19]. All these examples should lead to new studies about potential ethylene and auxin crosstalks in fruit set. These studies should cover the parthenocarpic fruit formation, which is becoming an important trait, offering a mean to ensure yield stability in unfavorable environmental conditions, these latter reducing pollen viability and depressing flower fertilization. Additionally, the epigenetic control is an emerging theme in developmental biology and its contribution to the fruit set process needs to be unveiled. It is therefore important to investigate how epigenetic components impact the transcriptomic reprogramming underlying different steps of fruit set. Finally, while the present review emphasizes the role of ethylene and auxin in fruit set, input from gibberellins is also critical to control this process [4,5]. Thus it will be interesting to expand the crosstalk studies to such hormones.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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